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STEM AND LEAF CUTICLE OF KARINOPTERIS: SOURCE OF CUTICLES FROM THE INDIANA "PAPER" COAL¹

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ABSTRACT

Cuticular or "paper" coal-shale is a local deposit of an organic-rich, highly clastic rock, with abundant leaf and stem cuticles, associated with the Upper Block Coal Member in Parke County, Indiana. Fresh blocks of cuticular coal can be split along bedding surfaces to reveal a fossil flora of low diversity, dominated by pteridosperms and lycopods, with minor amounts of ferns and sphenopsids. *Karinopteris* is a subdominant component of this flora and the great abundance of well-preserved cuticles of this plant allows for a reconstruction of its frond and growth habit. *Karinopteris* appears to have been a vine, indicative of structural diversity in the plant assemblage. The plant assemblage of the cuticular coal is dissimilar to most midwestern coal-ball floras of slightly younger age. This is probably a result of the depositional setting in an upper deltaic-fluvial dominated environment.

THE CUTICULAR or "paper" coal of Indiana is an unusual deposit rich in plant cuticles and intermediate in character between a bituminous coal and a highly organic shale. It occurs only as an upper facies of the Upper Block Coal Member of the Brazil Formation and has been located only in Parke County, in west-central Indiana. The cuticular coal was first reported in detail by Guennel and Neavel (1959) and Neavel and Guennel (1960). They speculated that the deposit represented a brackish or marine-influenced part of a more typical freshwater coal swamp. Their conclusions were based on elevated levels of boron and nickel in the cuticular coal facies, and on the abundance of plant cuticles in the deposit. Later studies were on the chemistry (Neavel and Miller, 1960) and the palynology (Guennel and Neavel, 1961) of this lithology.

Renewed interest in the cuticular coal was stimulated by its exposure during mining in Parke county. This was followed by reports of the general depositional environment (Eggert

and Phillips, 1982), palynology (Peppers, 1982), and paleobotany (DiMichele, 1980, 1982) of associated coals and shales, and petrology of the cuticular coal, which Crelling and Bensley (1980) found to consist of only 7.2% cutinite when fresh. Eggert and Phillips (1982) found no lithological or paleontological evidence of marine influence in the lower part of the Brazil Formation in Parke County. Further study suggests that the cuticular coal deposit is the result of the original plant composition of the coal swamp flora, in particular the abundance of the pteridosperm *Karinopteris*, perhaps reflecting unusual local ecological conditions within an upper deltaic fluvial environment (Nelson et al., unpubl., in review).

The cuticular coal is of specific interest botanically because of the unusual textural composition, caused by the abundance of cuticular material. Studies of both fresh and weathered specimens revealed that virtually all of the cuticle is derived from a single species of *Karinopteris*. This plant is a major component of a low diversity flora dominated by pteridosperms and lycopods. The morphology of *Karinopteris* is the focus of this paper; the associated flora will be described in brief.

Karinopteris is a form genus of pteridosperm foliage that has been reported infrequently in North America. Boersma (1972) established the genus and, based on specimens from western Europe, recognized a number of species previously included in *Mariopteris*, *Sphenopteris*, or *Diplothema*. *Karinopteris* is characterized by small, bipartite fronds that lack petiolar pinnules, have transverse marks on the

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rachises and stems, spinelike prolongations of the distal parts of the fronds, and pinnules with a mariopteroid or eusphenopteroid aspect (Boersma, 1972; Gastaldo and Boersma, 1983).

MATERIALS AND METHODS OF ANALYSIS—Fresh to slightly weathered cuticular coal and shale were collected within the now abandoned Roaring Creek Coal Company No. 1 Mine (7½' Wallace Quad., SE ¼, SW ¼, SW ¼, sec. 32, T.17N, R.7W) and from exposures on a steep cut bank along Roaring Creek at an elevation of about 560 feet above sea level (7½' Wallace Quad. SE ¼, NW ¼, NW ¼, sec. 33, T.17N, R.7W).

Additional highly weathered cuticular coal samples were obtained from an exposure in an abandoned strip mine near Nyesville, Indiana, in Parke County (7½' Rockville Quad. SW ¼, sec. 27, T.16N, R.7W); this was site A of Neavel and Guennel (1960). Samples of shale rich in cuticle were obtained along Sugar Creek at about 500 ft above sea level, near Coke Oven Hollow, Parke County (7½' Montezuma Quad. NW ¼, SW ¼, SE ¼, sec. 4, T.16N, R.8W). There were no coals exposed in association with this shale. At all locations collections were made from rocks of the Brazil Formation in the approximate stratigraphic interval of the Upper Block Coal Member.

Cuticle was removed from weathered cuticular ("paper") coal and shale, without chemical pre-treatment, directly from bedding surfaces. This technique occasionally yielded large pieces, but in most cases dense layering of the cuticle prevented removal of the significantly larger frond segments. Most cuticle was obtained by immersing hand-sized samples and larger pieces up to 20 cm a side and 1 cm thick in an aqueous solution of 5% KOH for 48 hr, followed by a 5-day rinse in gently running water. Specimens were subsequently treated with 32% H₂O₂ (superoxal), which rapidly (24 hr) disrupted the clastic matrix and released the cuticle. This solution was rinsed in gently running water for 48 hr. Cuticle then was hand separated or the mixture was sieved to remove the particulate material. Isolated cuticles were mounted in synthetic resin after dehydration in alcohol and xylene, or were mounted directly from water in Karo syrup.

A flora associated with the *Karinopteris* cuticle was studied from surfaces of fresh cuticular coal. Slabs split readily along horizontal bedding surfaces, due to the high clastic content of the coal, exposing compressions and impressions of stems, foliage and reproductive structures.

All materials are housed in the Paleobotan-

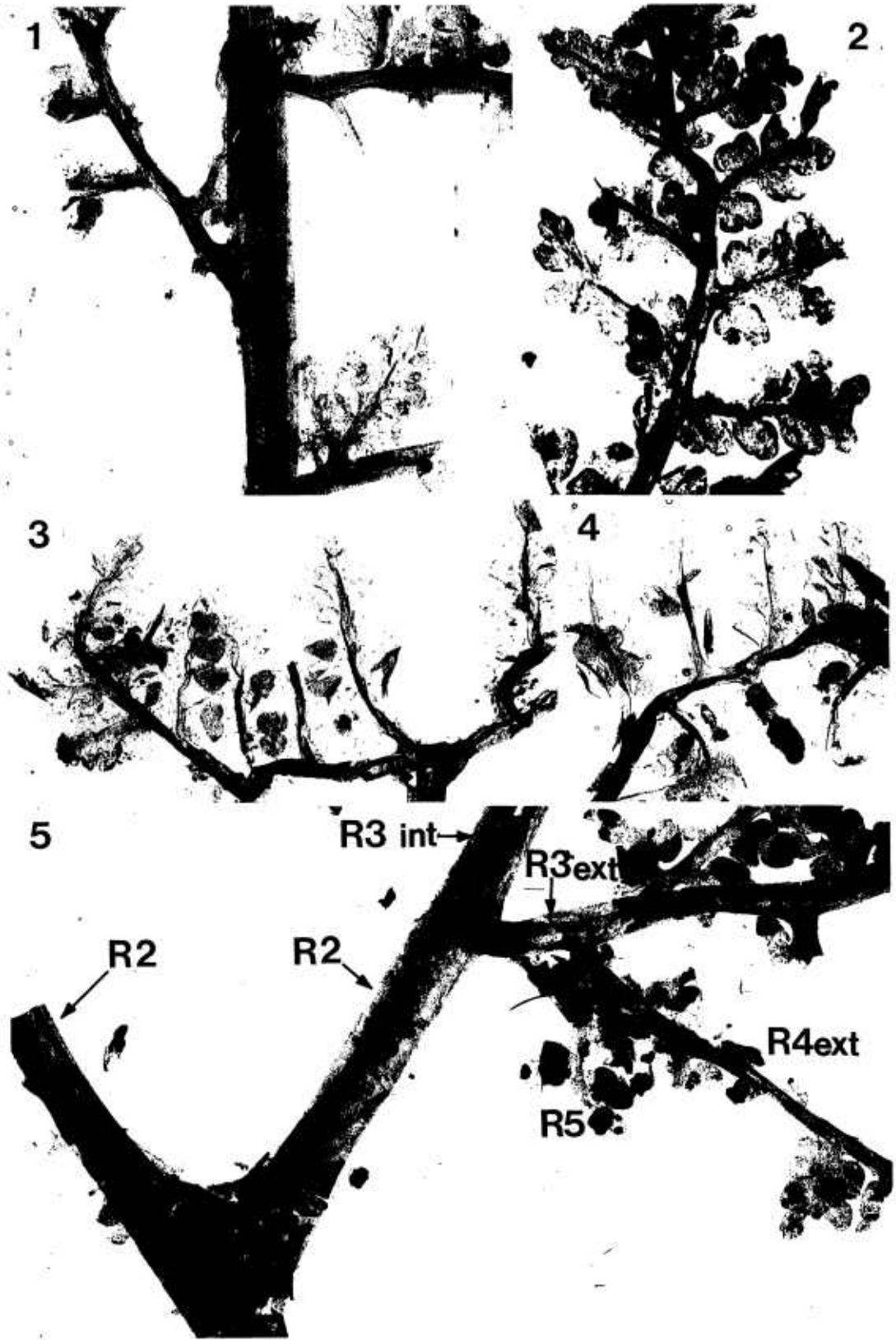
ical Collections of the University of Washington: Slides UW 00001–00155; Specimens RC 11.1–11.2, 14.1–14.9 (cuticular coal from Roaring Creek Mining Company, Mine No. 1), CO 1.1–1.21 (cuticular shale from along Sugar Creek in Coke Oven Hollow), and NYE 1.1–1.6 (cuticle coal from abandoned strip mine near Nyesville, Indiana).

MORPHOLOGY OF KARINOPTERIS SP.—*Nature of the fossils*—Almost all of the recovered cuticles represent fragments of the parent plant leaves and stems. Most material was leaf cuticle, from petioles to ultimate pinnules, that represents various segments of fronds (Fig. 1–7, 10). Large axes with remnants of horizontal sclerotic plates may represent stems or the basal portions of fronds (Fig. 8 and 9). Sporangial cuticle and spores of various sizes were common; these have been described and illustrated by Guennel and Neavel (1961) and are the only cuticular materials not associated clearly with the *Karinopteris* plant. Except for the sclerotic cell-plates in some of the larger axes, cellular material was absent, including vascular tissue. Cellular contents were macerated naturally from the cuticular envelopes or were coalified within the envelopes rendering them unrecognizable.

Description of the material—Four major kinds of fragmentary axes were obtained from macerations: terminal segments of fronds, mid-portions of fronds, basal frond segments, including dichotomized rachises, and large axes that probably represent stems.

The smallest diameter axes recovered were segments of frond rachises that terminated with spines. Four hundred and seventy-seven (477) spiny axes were found. They range from 0.3–2.0 mm diam, and average 1 mm diam (median 0.85 mm, Fig. 14). The spines are small and triangular in shape (Fig. 7). They are alternate and borne in two subopposite rows along the upper (adaxial) surface of a rachis. A few of the specimens, of the largest diameter in this group, 1.6–2.0 mm, terminate with an elongate, spinose segment (Fig. 6 and 7). Many of these specimens also bear lateral pinnulae below the terminal segment that are pinnulate, but terminate with spines rather than pinnules (Fig. 6, at arrows). Smaller diameter rachises, from 0.3–1.6 mm, are pinnulate along most of their length, but terminate with one or more spines. These are presumably ultimate or penultimate pinnulae, like those shown in Fig. 6, but that have been broken from the main rachis.

Four hundred and twenty-five (425) specimens were recovered in which a main rachis,



1.6–5.6 mm diam, bears one or more lateral pinnae, 1.1–2.0 mm diam. In many cases these primary lateral pinnae themselves bear additional pinnae, 0.5–1.0 mm diam, that bear pinnules (Fig. 1). Neither the primary or secondary pinnae are spinose. Diameter range of the main rachis was determined from all 425 specimens; attached to these were 711 primary pinnae, and to these, 143 secondary pinnae. Figures 2, 3, and 4 illustrate non-spinose, small-diameter rachises that bear an order of pinnae with pinnules. The size ranges of such axes are identical to those of non-spinose axes attached to the larger diameter rachises; they are probably detached primary pinnae from such frond segments.

Forked rachis segments (Fig. 5) were relatively rare. Twenty-three (23) were recovered from macerations. The petiole below the fork averages 4.7 mm diam, with a range of 2.0–7.5 mm. The two resultant rachis segments averaged 3.1 mm diam, with a range of 1.3–7.3 mm. These axes were usually unequal in diameter, differing by 0.1–0.9 mm, and averaging 0.2 mm diam difference. Eight were equal. Commonly, the resultant rachis segments were unequally forked again (Fig. 5, R3). This pattern of a near equal fork, followed by an unequal fork in the main frond rachis system, is characteristic of mariopteroid-karinopteroid fronds (Boersma, 1972). Pinnules were not found attached to any portion of the frond below the second major fork.

Many axes were recovered that bore no lateral axes or pinnules. These encompass a broad spectrum of size classes, including those within the pinnule-bearing parts of the frond. However, axes 0.75–2.0 cm diam were not found attached to pinnule bearing axes in any instances. They are interpreted as basal portions of petioles or as stems. Figures 8 and 9 illustrate large diameter axes; horizontal sclerotic plates, found in axes of all size classes, are particularly well-marked in these.

Pinnule venation is difficult to detect because the natural maceration process has removed most of the tissue of the leaf lamina, leaving the cuticle. Faint vein imprints are visible on most pinnules, and in some instances pyrite deposition in intercostal areas has accentuat-

ed the veins as clear regions (Fig. 10). Venation is sparse. One enters the base of a pinnule and dichotomizes usually once or twice, rarely three times, after entering the pinnule lamina. The result veins persist to the sub-marginal parts of the pinnule. Venation is most complex in the bilobed pinnules found at the base of each ultimate pinna.

Stomata are distributed on all cuticle surfaces, both axes and laminate regions, most abundantly above the vascular areas of the main rachis and lamina veins. It appears that the stomata were superficial. Guard cells are rarely preserved, and when present have resinous contents. Thus many stomata are represented by pores in the cuticle surface (Fig. 11). Such pores were interpreted as hair bases by Neavel and Guennel (1960); however, we have no evidence of hairs on any surface of the plant. There are no clearly differentiated subsidiary cells. Epidermal cells are elongate with smooth walls; the short, transverse walls are usually angular to the long axis of the cell. The epidermal cell patterns are detected most easily above veins and on rachises (Fig. 11).

Identification—Assignment of the cuticular material to *Karinopteris* is based on the following observations: 1) Presence of non-pinnulate terminal rachis segments bearing small spines (Fig. 6 and 7); in compression, where the small spines would be difficult to recognize, these rachis segments would appear as the smooth, “spinelike prolongations” noted by Boersma (1972) and Gastaldo and Boersma (1983) in *Karinopteris*. 2) Presence of horizontal sclerotic plates in rachises and probable stems (Fig. 8 and 9) that correspond to the transverse marks on compression specimens of *Karinopteris*. 3) Evidence of one major frond-bifurcation, followed in each resultant rachis by a much smaller bifurcation (Fig. 5), a pattern typical of *Karinopteris*. 4) Pinnules with angular insertion, sparse venation, and an angular-ovoid shape (Fig. 2–4 and 10), intermediate between many species of *Mariopteris* (with more triangular pinnules, Boersma, 1972), and *Eusphenopteris* (with pinnules having more oval lobes, van Amerom, 1975).

The cuticular coal material does not conform

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Fig. 1–5. *Karinopteris* foliage. 1. Fragment of frond showing primary and secondary pinnae and pinnules attached to large diameter axis, one of two main (R3int) frond segments. 2–4. Fragments of pinnae bearing pinnules, illustrating variation in pinnule shape. Note that basal pinnules on both proximal and distal sides of ultimate pinnae are usually bilobed. 5. Y-shaped, dichotomized axis, presumed to be the single major bifurcation from the lower part of a frond, R2, R3int, R3ext, R4int and R5 refer to progressive branch orders of frond. See text for explanation. All specimens magnified $\times 3$.

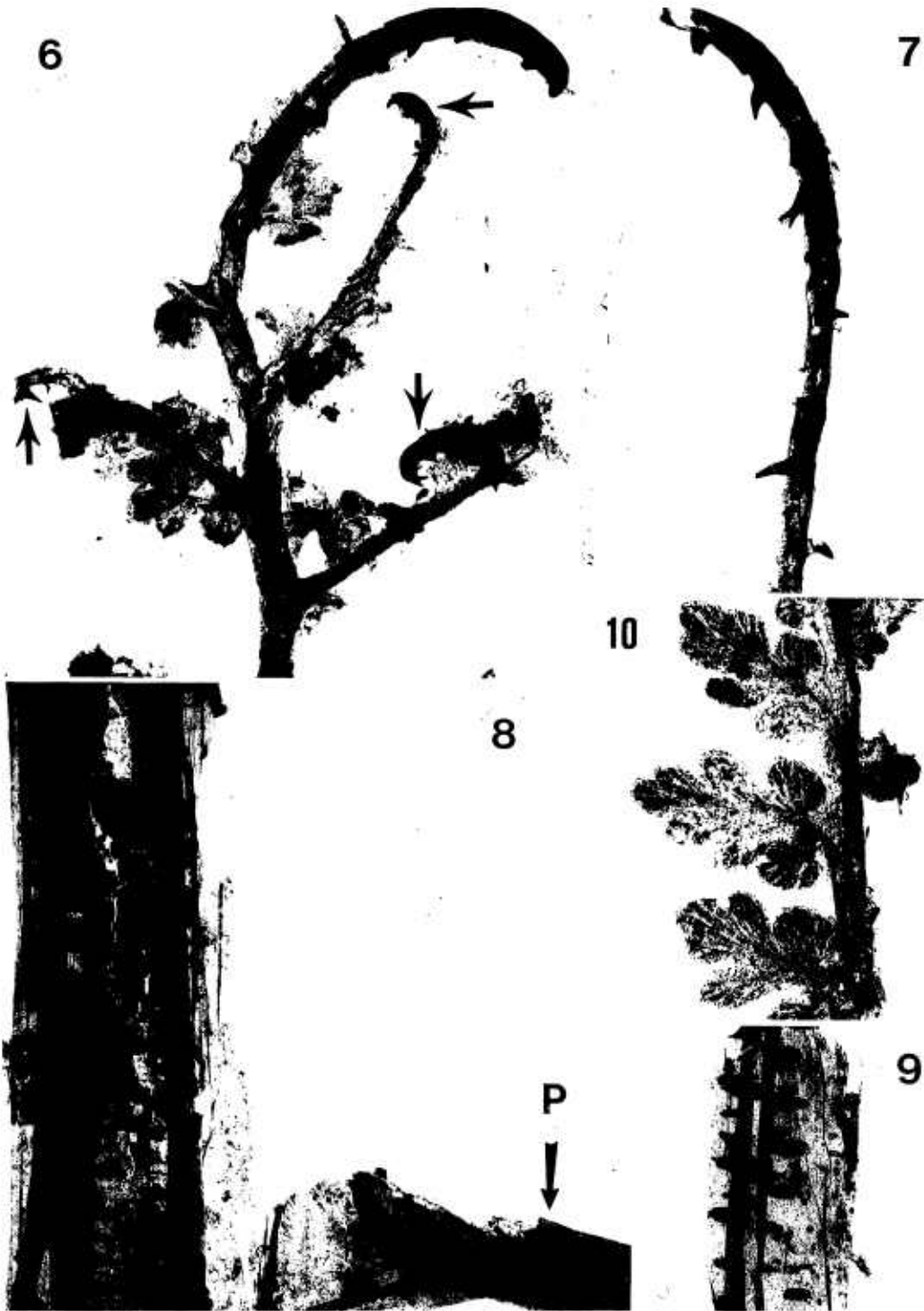


Fig. 6-10. *Karinopteris* foliage and stems. 6. Terminal segment of rachis with spine-like appendages. Pinnule bearing ultimate pinnae also terminate in spines (arrows). 7. Terminal segment of rachis with numerous, well-developed, spinelike appendages. 8. Large-diameter axis bearing a smaller axis (P). Small axis is interpreted as a petiole base, large axis as a stem. Some carbonized material remains in the cuticular envelope of the stem. 9. Axis, interpreted as a stem because of large diameter, with remnants of horizontal sclerotic plates. 10. Pinnules with pyrite deposited in intercoastal areas, emphasizing the vein patterns (clear areas). One or two veins enter the base of the pinnule lamina and bifurcate one to three times. Fig. 6-9, $\times 3$; Fig. 10, $\times 7$.

precisely to any of the species described by Boersma (1972) or Gastaldo and Boersma (1983). However, description of a new species seems inappropriate because entire fronds are not preserved and because range of variation for most of the described species is not yet appreciated. Closest comparisons can be made with *Karinopteris acuta*, *K. soubieranii*, *K. nobilis*, and *K. dernoncourtii*. Pinnules of *K. acuta* are more narrow and acute at the tips, are more widely separated along the ultimate rachises, and have more orders of vein branching, and hence higher vein density, than the cuticular coal specimens. *Karinopteris soubieranii* and *K. dernoncourtii* present relatively close comparisons because of the eusphenopteroid form of their pinnules. *Karinopteris soubieranii* differs from the cuticular material in having more rounded pinnule apices, much more branching of lamina veins, hence a higher vein density, and in general a more robust frond construction, all aspects being larger than in comparable specimens from the cuticular coal. *Karinopteris dernoncourtii* also is larger than the cuticular coal species. It has more acute pinnule shape and higher vein density in the pinnules (Danze-Corsin, 1953). *Karinopteris nobilis* is similar to cuticular specimens in the sparsely bifurcate venation of the lamina. In addition, the "compression border" of *K. nobilis* may be a consequence of thick cuticle, which would compare well with the cuticular specimens. However, pinnule shape of *K. nobilis* is more deltoid, pinnules are larger in general, and there is no evidence of abaxial hairs, characteristic of *K. nobilis*, in the cuticular material. Of these comparisons, *K. soubieranii* and *K. nobilis* are most similar to the cuticular specimens on the basis of general pinnule morphology, but in different aspects; neither appears to be an ideal choice for identification and we have chosen to identify the cuticular specimens as *Karinopteris* sp.

Reconstruction of the frond—Identification of the cuticular material as *Karinopteris* provided a generalized architectural plan for reconstruction of the frond (Boersma 1972). The reconstruction (Fig. 12) is based on isolated fragments and thus is, in part, hypothetical. Boersma (1972) and Gastaldo and Boersma (1983) have developed and utilized a strict and consistent terminology for mariopteroid frond-branch orders that is used here. R1 refers to the petiole, below the first major fork of the frond. R2 designates the two resultant axis segments up to the next, and highly unequal frond bifurcations. The interior, ascending axis of the second bifurcation is designated R3int; it is

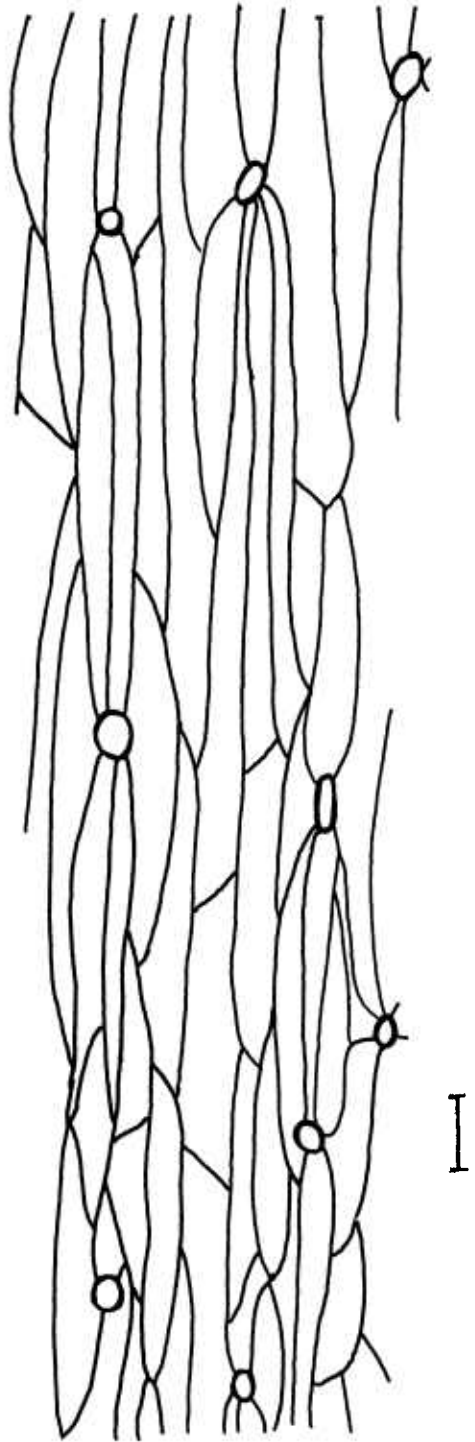


Fig. 11. *Karinopteris* epidermal pattern. Camera lucida drawing of epidermal pattern from pinna axis. Oval openings are remnants of stomata. Pattern is typical for areas above veins in pinnules or on rachises. Scale = 50 μ m.



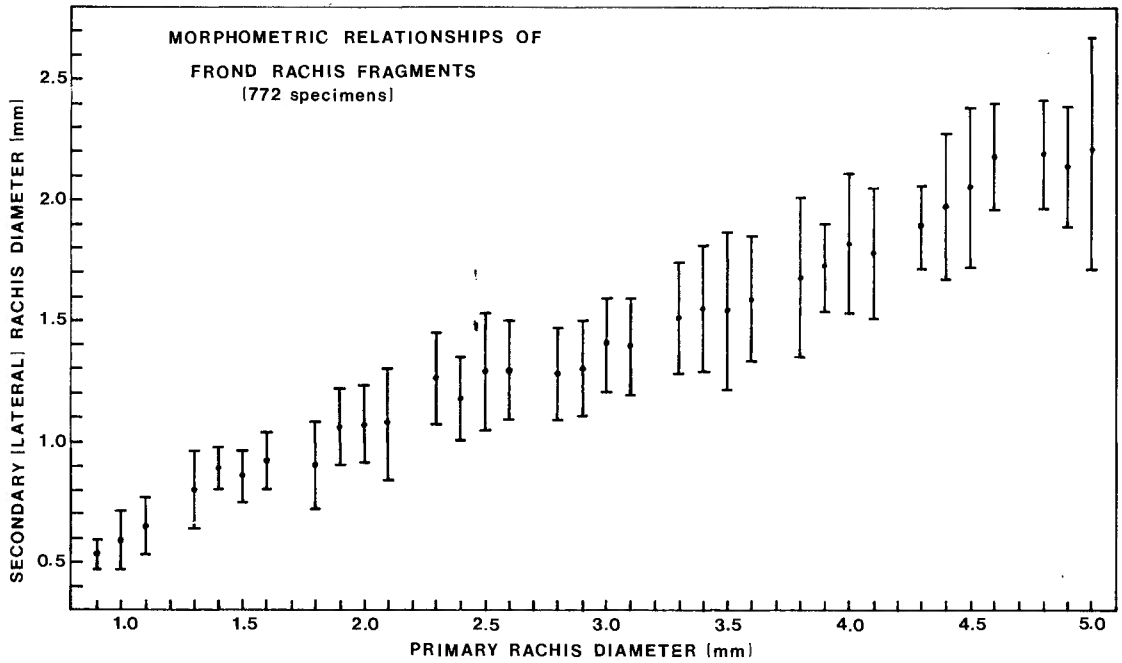


Fig. 13. Relationship between diameter of a rachis or pinna fragment (abscissa) and the mean diameter of lower order pinnae attached to it (ordinate). Bars indicate standard deviations of y .

one of the two major rachises of the bilateral frond. R3ext refers to the minor resultant axis of the second bifurcation on each side of the frond. Subsequent orders of pinnae are designated R4, R5 etc., with interior or exterior giving the position relative to the line of symmetry through the center-line of the frond. Figure 5 illustrates this frond-segment terminology.

In reconstructing the frond, fragmentary material first was ordered into size classes based on the diameter of the largest axis. The number of branch (pinna-rachis) orders present in each specimen then was determined, and the diameter of the axis from which each successive branch originated (Fig. 13). Specimens that are approximately equally forked (Fig. 5) are considered to be major (R2) dichotomies of the rachis, and provide some indication of the general size of the frond. Pinnule bearing segments with > 1 rachis order (Fig. 1-7) were considered to be portions of one of the two major acroscopic frond rachises (R3int), or part of the first subsequent rachis derived from R3int (R3ext) (Fig. 5). R3ext rachises frequently show a

prominent basal, basicopic rachis (R4) that bears the ultimate pinnae (R5) (Fig. 5). Spinous tips were found only on specimens that appear to be from terminal parts of the frond (Fig. 6 and 7).

On the basis of 772 specimens there is a positive relationship between increase in diameter of any rachis or pinna and diameter of pinnae attached to it (Fig. 13). This is probably indicative of the general determinate nature of the frond. Points in Fig. 13 are based on fragments of fronds, and represent the average size of axes attached to a parent axis in each size class; standard deviation is given for each point. The relatively low slope of this line, approximately 0.45, indicates that variation in diameter of lateral pinnae (0.5-2.3 mm) is much less than that of the major rachises. The range of size in penultimate and ultimate pinnae, even if borne on large, robust R3int rachises, is relatively limited. The size of the pinnule-bearing pinnae and those to which they are immediately attached suggests that there were some structural limits on the size of the frond.

The frequency of unequally forked basal

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Fig. 12. Reconstruction of frond based on isolated cuticle fragments. Dotted lines mark limits of specimens used in the reconstruction. Basic shape and size of hypothetical frond were designed to correspond to the observed distribution of specimen dimensions and shapes, and the general architecture of a *Karinopteris* frond. Scale = 1 cm.

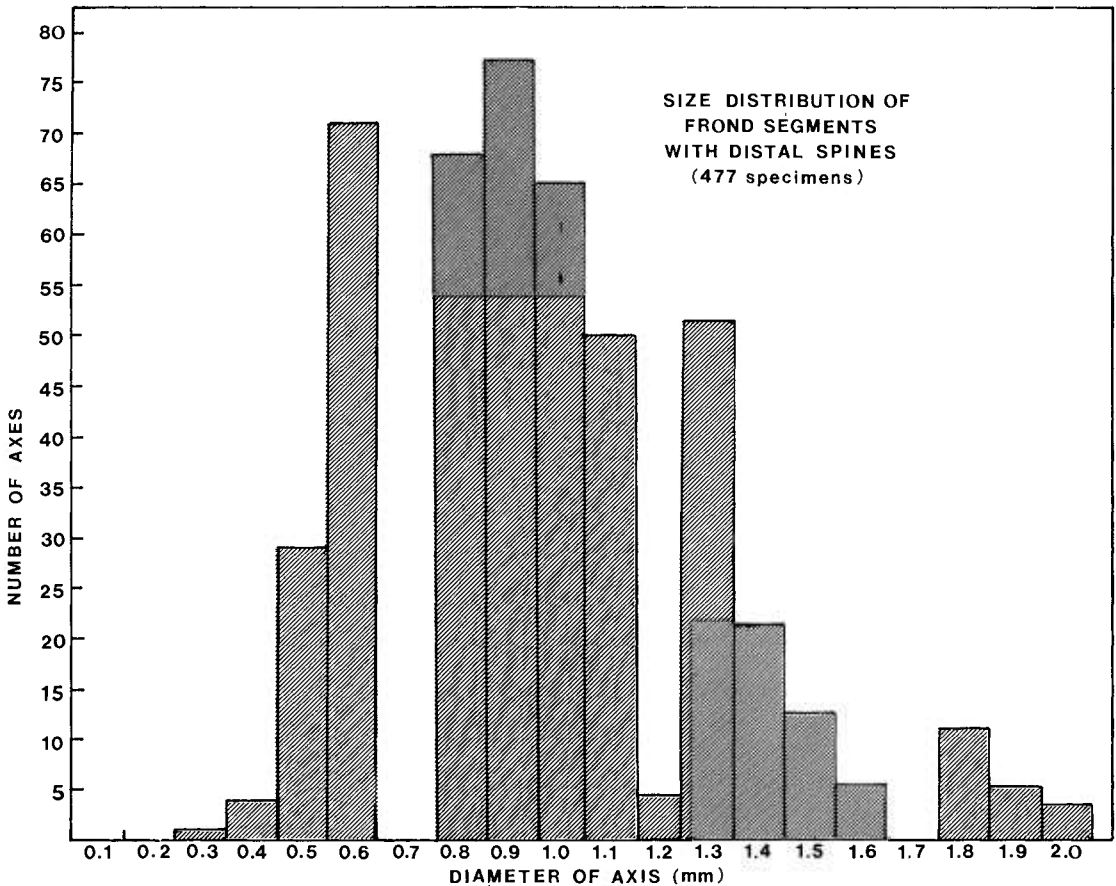


Fig. 14. Diameter classes of axes terminating with one or more spinelike appendages.

frond segments suggests that most fronds were not evenly bilaterally symmetrical. One side of the frond may have been considerably more robust than the other. In addition, the relatively large range in diameter of the top of the petiole (2.0–7.5 mm) and in the diameter of the resultant R2 axes (1.3–7.3 mm), especially considering the small sample size of these fragments ($n = 23$), suggests considerable variation in overall frond size on mature plants. Petiole length could not be determined.

The smallest diameter axes in all cases terminate in a naked rachis segment that bears small, spine-like appendages rather than pinnules or a terminal pinnule; the size distribution of these is shown in Fig. 14. Axes 1.6–2.0 mm diam that end in a highly spinose segment are probably the terminal segment of R3int rachises. Spines appear to represent modified or unexpanded pinna or pinnule primordia, because they are positioned in the same way as these appendages are throughout the rest of the frond. The “spinelike prolongations” reported in the distal parts of *Karinopteris* fronds

represent these spiney, non-pinnulate termini of various rachis branch orders. The small spines usually are not seen in compression, thus the entire axis had been interpreted as a smooth, spinelike terminus.

Large axes, from 0.8–2.0 cm diam, are interpreted as stems, and possibly the basal portions of petioles. They frequently have horizontal areas of dark cells (Fig. 8 and 9), probably sclerenchyma, that are fusiform in shape and are probably equivalent to the horizontal sclerotic plates of some other pteridosperms.

ASSOCIATED FLORA—*Karinopteris* was a component of a more diverse vegetation, and did not grow in pure stand. Floral composition was determined by subsplitting nine blocks of cuticular coal collected from Roaring Creek Coal Company Mine No. 1. The following elements have been identified: *Lepidodendron aculeatum*, *Sigillaria brardii*, *Karinopteris* sp., *Pecopteris miltonii*, *Alethopteris ambigua* (? *davreuxii*), *Calamites carinatus*, ? *Neuropteris obliqua*, *Sphenophyllum* sp., and numer-

ous small pteridosperm ovules (6×5 mm). Qualitatively, pteridosperm axes with longitudinal sclerotic bundles, characteristic of Medullosan pteridosperms, are the most abundant element. Lycopod bark sheets are second in abundance. *Karinopteris* is exceptionally abundant in some layers a few millimeters thick, and it occurs dispersed throughout the entire cuticle coal matrix. *Alethopteris ambigua* is the second most abundant foliage-type and occurs on some bedding surfaces in great abundance. *Pecopteris* is scattered and there is some evidence, although difficult to interpret, of *Psaronius* stems (coarsely, irregularly longitudinally striated axes). Foliage, except for the *Karinopteris* cuticle, is fragmentary, probably as a result of local transport or decay.

The diversity of this flora is low in comparison to penecontemporaneous associated gray shales. It parallels the diversity and nature of the flora found in shale partings within a coal seam lower in the local section that Peppers (1982) has identified tentatively, on the basis of palynology, as in the same stratigraphic interval as the Mariah Hill Coal Bed of the Mansfield Formation.

DISCUSSION—*Karinopteris*—Reconstruction of a complex frond such as that of *Karinopteris* from extremely fragmentary material is based upon a series of deductions. The first requirement is, of course, proper identification of the material, which allows the fragments to be fit to a satisfactory archetype. In the lack of contradictory material, it appears that the basic *Karinopteris* frond (Boersma, 1972), with a single major dichotomy of the rachis, is an acceptable model.

The most puzzling aspects of the morphology are the spinelike protrusions found on the terminal portion of the rachis and at the tips of lateral pinnae in the distal portions of the frond. The relationship of diameter of successive pinna/rachis orders suggests that the fronds were determinate; thus it is unlikely that the spines are evidence of a still juvenile condition (i.e., unexpanded pinna primordia) in an indeterminate frond. Since we recovered no exceptions to spines on terminal rachises we must reject the idea that all leaves were shed and preserved prior to complete development. The most likely remaining conclusion is that in the fully developed state, at the tips of virtually all fronds, pinnule/pinna primordia were altered and matured as spine-like protrusions.

Spinelike structures appear to have been present in all *Karinopteris* species. Since the spines clearly did not evolve "for" any function, the ultimate survival of such a character

may have depended on the habit of the plants bearing it; post-appearance adaptiveness, if any, would seem to be most likely in a vine, where the spines may have allowed leaves to support an extended canopy. The small size of the fronds and their wide spacing on stems (Boersma, 1972; Gastaldo and Boersma, 1983) lend support to interpretation of a liana habit (Remy and Remy, 1977; Boersma, pers. commun. to Gastaldo). A liana habit would imply a relatively high structural diversity of the vegetation with a complex canopy capable of supporting abundant vines. Assuming that the cuticle-coal flora is hypoautochthonous, not highly transported, there is indeed suggestion of structural diversity that includes several arborescent pteridosperms, two arborescent lycopods, tree ferns and arborescent sphenopsids. Low taxonomic diversity may reflect sampling and the difficulty in recognizing many of the smaller plants that may have been components of the flora, rather than true low diversity (i.e., the major components only may have been sampled; Scheihing, 1980).

Karinopteris compares favorably with the structurally preserved plant *Schopfiastrum* (Rothwell and Taylor, 1972; Stidd and Phillips, 1973). Stems and fronds of *Schopfiastrum* were of small size and the axes had horizontal sclerotic plates in the outer cortex. The frond had a major Y-shaped fork below the pinnulate portion, and, although known only from fragmentary material, pinnules are not inconsistent with those known from *Karinopteris*. *Schopfiastrum* may have been a liana; it is rare in coal balls and often is fusinized (charcoal). Lianas were probably an important part of most coal-swamp floras. Plants reconstructed with scrambling or liana habit include *Callistophyton* (Rothwell, 1975, 1981), which had *Dicksonites pluckenetii* foliage (Stidd and Barthel, 1979), *Heterangium*, which frequently is fusinized, has horizontal sclerotic plates in the stem, and *Eusphenopteris obtusiloba* foliage (Shadle and Stidd, 1975), a number of small, "coenopterid" ferns (Phillips, 1974), and possibly some cordaites (Costanza, 1983; Rothwell and Warner, in press). However, these have not been reported to reach abundances comparable to that of *Karinopteris* in the cuticular coal.

Cuticular coal—The flora of the cuticular coal differs in a number of ways from known Euramerican coal-swamp floras, which, in the Middle Pennsylvanian, were dominated by lycopods or cordaites (Phillips, 1980). The cuticular coal flora has more similarity to a compression flora, representing vegetation of

mineral substrate environments, than a coal-swamp flora as known from coal balls. This is not unexpected because the clastic content of the cuticular coal is very high (11–50%) and the deposit has a distinct shaley cleavage. This implies either a high clastic influx into the swamp, or, perhaps, a high peat decay rate that concentrated the clastics. In either instance the environment would have differed from the typical peat-accumulating swamp. Unusual botanical aspects of the cuticle coal include the abundance of *Lepidodendron aculeatum*, usually very rare in coal swamps (DiMichele, 1983), and the general predominance of pteridosperms. Pteridosperms only rarely were quantitatively significant in Middle Pennsylvanian coal swamps (Phillips and DiMichele, 1981), and were subdominant to tree ferns in the Late Pennsylvanian (Phillips, 1981). *Lepidodendron aculeatum*, a diversity of medullosan pteridosperms, and *Pecopteris miltonii*, also a cuticular coal component, are all elements in the gray-shale floras of the local section. Of other components, *Alethopteris ambigua* has been found locally only in the cuticular coal or in organic-rich shale partings of other coals; its occurrence may be linked to swamps with either low clastic influx or high levels of peat decay. *Karinopteris* occurs either in the cuticular coals or in shales and coarse silt-stones immediately above the coals. The presence of a thick cuticle in *Karinopteris* sp., in and of itself, gives little or no indication of the kind of environment in which the plants may have grown, or the nature of the vegetation of which they were a part.

The cuticle coal deposit contains relatively little cuticle from plants other than *Karinopteris*. This suggests that the abundance of *Karinopteris* sp. in the parent vegetation is the underlying cause of this unique lithology, and not differential depositional conditions that favored the preservation of cuticle. Its formation as an upper bench of an otherwise typical bituminous coal may have resulted from changing edaphic conditions as peat accumulation filled in poorly drained lowland areas. This would have ameliorated the edaphic constraints imposed by a peat substrate as, for whatever reason, clastics became more concentrated in the peat and allowed the development of a more typically "compression" vegetation.

The limitation of this kind of deposit to such a small geographic area is puzzling, and is possibly a consequence of local paleoenvironmental conditions. The general depositional environment in the area appears to have been strongly controlled by topographic factors and nearby freshwater sources (Nelson et al., in

review), which is different from that of most lowland Pennsylvanian coal-forming environments in the Illinois Basin. Most coal-ball floras of the Illinois Basin are from coal seams that formed in large lower-delta-plain or coastal swamps. Eggert and Phillips (1982) and Nelson et al. (submitted) recognized that in the Parke County area the Upper Block coal and the associated cuticular coal-shale formed in an upper delta plain setting that was influenced highly by nearby fluvial channels. The Upper and Lower Block coals in general are duller with lower vitrain content than younger Indiana coals (Neavel, 1961). They have greater petrographic similarity to coals of the Appalachian Region than to coals such as the Springfield and Herrin Coal Members of the Illinois Basin (Harvey et al., 1979), which formed in large coastal, deltaic swamps. Thus, it is possible that the petrographic and floristic differences between the Upper Block-cuticle coal and the later Illinois Basin coals is due, in large part, to the differences in depositional setting. *Karinopteris* and the associated plants found in the Upper Block coal, the cuticular coal-shale, and gray shales in Parke County, Indiana add further evidence for recognition of the variability and temporal changes that occurred in environmental settings of coal swamps during the Pennsylvanian within the Illinois Basin. They are an important link between earlier and later coal-swamp floras and represent a time interval for which we have limited coal-ball evidence of coal-swamp vegetation patterns.

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